

NOTES ON THE PHYLOGENY OF LIRIODENDRON

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(WITH ONE FIGURE)

THERE are many reasons why the tulip tree is an object of unusual interest, but its scientific interest chiefly arises from the facts that, like the *Sequoia*, *Sassafras*, *Platanus*, *Ginkgo*, etc., it is the lone survivor of an ancient race extending back into the Cretaceous period, that most of the race history can be traced, and that we find this history epitomized in the existing species.

Liriodendron Tulipifera is confined to the eastern portions of North America and Asia, although it or its probably identical representatives were common in Europe during the Tertiary period. Like other trees peculiar to North America at the present time, such as *Magnolia*, *Liquidambar*, *Sassafras*, etc., and which inhabited Europe during the Tertiary, it was forced to the Mediterranean by the glaciers and exterminated. The existing Asiatic form has been described as a variety (*chinensis*¹), but it is very doubtful whether it is distinct. In North America the tulip tree is found from Vermont to Florida and westward to Michigan and Arkansas, and appears to be confined to the humid temperate realm, requiring a rich soil for its full development.

The great variability among the leaves of the tulip tree, as well as the resemblance of some of them to fossil species, has attracted very little attention, possibly, as Holm suggests,² because this variability is so well known as not to merit discussion. The belief that this is not the case has led to the following notes, extending over a number of years, and based upon innumerable specimens. While these notes are incomplete and

¹ Descriptions of some new phanerogams collected by Dr. Shearer in China, etc., Jour. Bot. 13:225. 1875.

Enumeration of all plants known from China, etc. F. B. Forbes and W. B. Hemsley. Jour. Linn. Soc. 23:25. 1886.

² Proc. U. S. Nat. Mus. 13:15-35. 1890; BOT. GAZ. 20:312. 1895.

disconnected in many ways, it has seemed best to arrange and present them.

A common error is the belief that a truncate or emarginate apex is a constant feature, induced, no doubt, by a consideration of the vernation, which would seem to preclude any other form of apex, and which has been the subject of papers by Lubbock³ and others. Lesquereux⁴ says "leaves always truncate or emarginate at the apex," and Newberry⁵ makes the same statement. Holm,⁶ in his paper on the leaves of *Liriodendron*, goes still further, and insists that the notched apex is the true test of the genus *Liriodendron*, and hence unnotched leaves or forms with the apex of the leaf missing cannot be identified with certainty; and Hollick⁷ makes the statement that the apex is always cuneate or notched. Doubtless others have followed the lead of these authorities.

I have collected numerous leaves of *Liriodendron Tulipifera* with pointed tips, and I have also a number of similar specimens collected by Mrs. W. A. Kellerman, of Columbus, O., showing how fallacious the above cited criterion proves. Among my collections of these anomalous forms may be noted a simple obovate leaf closely resembling *Phyllites obcordatus* Heer; a trilobed form identical with *Liriodendron semialatum* Lesq. of the Dakota group; a small leaf unlike anything before known in this genus and almost exactly corresponding with *Cissites acuminatus* Lesq., pl. 5, fig. 3, of his *Cretaceous and Tertiary Floras*; a large trilobed leaf which is also a new form in the genus and recalls Heer's *Aralia groenlandica*; also numerous ovate-lanceolate leaf blades on leaf bearing flower buds (see fig. 3). The foregoing examples are sufficient to refute the claim that the notched apex is an essential character, and we should expect to find just such leaf forms if we accept the origin of *Liriodendron* from forms with simple, magnolia-like leaves. Fossil species based on leaf forms

³ Phytobiological observations. Jour Linn. Soc. 22: 24. 1887; and GODRON, A., Obs. sur les bourgeons et sur les feuilles des *Liriodendron Tulipifera*. Bull. Soc. Bot. France 8: 1861.

⁴ Flora of Dakota group, p. 229.

⁶ Proc. U. S. Nat. Mus. 13: 1890.

⁵ Flora of the Amboy clays.

⁷ Proc. Nat. Sci. Ass. Staten Is. 5: no. 7. 1896.

alone are always more or less problematical, and yet in many cases form alone has served for specific distinction.

Venation also is much depended upon in defining species, although both venation and leaf form are characters which vary in a marked degree in the modern tree, even on the same individual. Leaving out the anomalous forms from shoots, forced buds, saplings, etc., almost any sassafras or tulip tree will show a more or less wide variation among mature leaves on branches which theoretically (*i. e.*, fruiting branches) should bear typical leaves; and when we compare a series from different trees or of different ages the variation in shape and minor characters of venation is almost endless. Perhaps no style of venation is more characteristic generically than the peculiar form that obtains in *Liriodendron*. That it cannot be relied upon for specific distinctions we know from its wide variation on the living tree, as well as among the fossil species referred to this genus. In some specimens the secondaries are opposite instead of irregularly alternate; in some they are parallel almost to the margin and ascending; while in others they soon divide. The angles of divergence of the secondaries show every degree of divergence, acute angles, right angles, or obtuse angles. All that should be claimed for venation characters, generally speaking, is usefulness in generic distinction or as supplementary evidence in connection with species.

Holm considers nearly all of the described forms of *Liriodendron* invalid, while most authorities consider nearly all of them perfectly good species. Professor Ward's dictum, that for geological purposes it is not so much a question of correct botanical determination as the correct recognition of a plant once named and associated with a given deposit, is quite true; but it loses its force when we are considering forms with variable leaves, unless each variety is constant and peculiar to a given formation, which is obviously not the case. In pursuing the comparison through the intermediate forms of ancient *Liriodendrons*, who can say where to break the chain of gradations for the boundary of separate species; among the gradual modifications of form, strikingly similar to

a series of leaves of *Liriodendron Tulipifera*, who can say where *L. simplex* ends and *L. primaevum* or *L. Meekii* begins, or where *L. primaevum* ends and *L. semialatum* begins? The same variability and interrelation is shown among the leaves variously referred to *Aralia*, *Sterculia*, *Cissites*, *Menispermities*, *Protophyllum*, *Platanus*, *Sassafras*, etc.; and, while it may be argued that we should expect just such variable and intermediate leaves at a time when the flora of the globe was becoming rapidly differentiated, the argument loses force when we turn to a similar variability and interrelation of the modern forms of the same genera, when their leaves alone are considered.

In considering the thirty or more species and varieties of fossil forms ascribed to *Liriodendron* and its allies *Liriodendropsis* and *Liriophyllum*, we may distinguish them as all good species, or as three or four, or we may identify most of them with the modern form, dependent upon our conception of the term species. If the Cretaceous period, at the time the Dakota strata were being laid down, was the time of maximum development and diversification of the dicotyledons, it is difficult to understand how so many of the types are still persistent with all their essential characters unchanged (*Myrica*, *Betula*, *Quercus*, *Populus*, *Viburnum*, *Salix*, etc., and representatives of nearly all of the natural orders), even in some cases to specifically similar forms (as *Magnolia acuminata* and *M. tripetala*). If there was such a diversification of species at that time as we are led to believe, it is strange that most of the types persist comparatively unaltered through the later formations to the present time, instead of losing their character in further continued variation.

We have listed as follows a few of the reasons for considering some or all of the described species of *Liriodendron* invalid:

1. Their remains are more or less fragmentary, and therefore not determinable with certainty.
2. The shape and venation of leaves are poor specific characters at best.
3. A series of leaves of *Liriodendron Tulipifera* can be found which parallels the fossil species in both shape and size.

4. There is a close intergradation among the various fossil forms.

5. The more unusual fossil forms are mostly small leaves, and it is among the smaller leaves on shoots and saplings of *Liriodendron Tulipifera* that we find the most diverse shapes, and those forms which most resemble the diverse fossil forms.

6. The remains of different fossil species would be unlikely to occur associated with each other.

7. *Liriodendron* is a monotypic genus at the present time.

8. The existing tulip tree very probably extends back into the Tertiary period, there being no great climatic change except during the Glacial period, which was survived by all of our existing arboreal vegetation. It is not stretching a point, therefore, to assume that our existing species of *Liriodendron* might extend still farther back into the Cretaceous; other plants do (*Magnolia*), and paleontology affords many examples of such persistent animal types.

9. Nearly all of the fossil forms of *Liriodendron*, if found at the present time, would be unhesitatingly referred to *L. Tulipifera* from a consideration of their leaf form alone; and practically all of the abnormal leaf forms of *L. Tulipifera*, if found as fossils, would be considered distinct species.

10. If we assume that in the ancient forms of *Liriodendron* the largest and best developed trees were on hillsides, as is the case in the modern tree, then the smaller, more aberrant forms, which occur on vigorous saplings and shoots, inhabiting the more marshy situations, would be the forms mostly likely to become fossil.

11. A warm, humid climate during the Cretaceous might account for the variety in shape and size of the leaves, just as in *L. Tulipifera* the best nourished individuals are the most variable.

12. The fact that so many of the fossil forms were contemporaneous militates against considering them as different stages in the development of the genus. We might with equal propriety consider the existing varieties as actual stages.

13. The barren record of the Tertiary period would seem to

imply that the diverse forms are found in the Cretaceous simply because the conditions were favorable for the fossilization of the abnormal forms.

In opposition to the foregoing, our reasons for considering the various described species valid are:

1. The majority of abnormal leaf forms in the living *L. Tulipifera* are young leaves, and they would not be likely to become detached and preserved as fossils.

2. We have every reason to expect numerous species in a tree ranging over so many lands (Europe, Asia, America), and throughout such a long period of time (Lower Cretaceous to the present).

3. The Cretaceous was a period of development and variation in the dicotyledons.

4. Ontogeny, or the individual development of modern types, more or less parallels their phylogeny, or actual ancestry. Generally speaking, this applies to all animals and plants.

5. The weight of authority is all on the side of many species, Lesquereux⁸ going so far as to say "from the remarkable diversity of characters seen in the leaves of *Liriodendron* described in this volume, I believe that no botanist would be disposed to consider them as mere varieties of the original obovate simple leaves." In criticising Holm's paper on *Liriodendron*, Professor Lester F. Ward⁹ says "modern forms more likely represent the phylogenetic stages through which the present living species has passed." This is the view held by all, so far as I know, of the various authors who have written of this group, as Newberry, Lesquereux, Hollick, etc., in this country, and Heer, Ettingshausen, Unger, Saporta, Velenovsky, Massalongo, etc., abroad.

6. If stipules were present—and they must have been, since *Liriophyllum populoides* of the Dakota and *Liriodendron alatum* of the Laramie show their incipient stages—they should occur as fossils, either separately, if we assume them to have been fugacious, as they are at the present time, or attached to the petioles of the fossil leaves, if they were persistent.

⁸ Flora of Dakota group, pp. 205, 206.

⁹ Am. Jour. Sci. III. 40: 422. 1890.

In reply to the question whether each one of the described species of *Liriodendron* represents a definite species established in nature, we are compelled to answer in the negative; for the evidence that the majority of these forms were distinct species, in any proper sense, is entirely insufficient. At the same time, we are led to believe, from a study of these fossil forms in conjunction with the modern form and its varieties, that *Liriodendron* in the course of its evolution has passed through a series of parallel stages, as we will endeavor to show. It matters little whether we call these stages species or stages.

The purpose of Holm's¹⁰ paper on *Liriodendron* is stated as follows: "The object of these notes . . . is to prove that, as far as is known to the writer, there is not a greater difference in the foliage between many of the extinct species of *Liriodendron* than between a series of leaves from a very young tree or from a branch of an older one of our living *L. Tulipifera*;" and he then proceeds to attack the validity of the various species. Since 1890 a host of specimens, including many interesting forms,¹¹ have come to light, and much new material has been published. Two works in particular may be mentioned, the last labors of the pioneers Lesquereux¹² and Newberry¹³ being issued posthumously, as well as various contributions from Hollick and others on the plant remains from Long and Staten islands and elsewhere. The time seems opportune for recording some additional notes, and correcting several current inaccuracies. It is far from the purpose to attempt to diminish or increase

¹⁰ Proc. U. S. Nat. Mus. 13: 16. 1890.

¹¹ The following new species: *Liriodendropsis angustifolia* Newb., *l. c.*, p. 84; *Liriodendron alatum* Newb., Hollick in Bull. Torr. Bot. Club 21: 467. 1894; *L. acuminatum bilobatum* Lesq., *l. c.*, p. 207; *L. Snowii* Lesq., *l. c.*, p. 209; *L. succedens* Dawson, Trans. Roy. Soc. Canada 11: 62, pl. 8, fig. 26. 1893 (1894); *L. praetulipiferum* Dawson, *l. c.* fig. 27; and the winged petiole forms of *Liriophyllum populoides* Lesq., Hollick, *l. c.*

¹² Flora of Dakota group, edited by F. H. Knowlton. Monograph 17 U. S. Geol. Surv. 1891.

¹³ Flora of the Amboy clays, edited by Arthur Hollick. Monograph 26 U. S. Geol. Surv. 1895.

the number of described forms of *Liriodendron*, and so needlessly encumber the synonymy.

In comparing the ancient types of *Liriodendron* with the modern varieties of *L. Tulipifera*, the purpose is to establish the fact that those ancient forms of leaves which were simple, or with unnotched apices, or with winged petioles, and which some authorities are inclined to exclude from *Liriodendron*, are undoubtedly correctly identified as primitive forms of that genus.

THE EVOLUTION OF LIRIODENDRON.

Following Holm, we would consider the primitive ancestral type of *Liriodendron* to have been a simple, Magnolia-like leaf; for not only do all the modern relatives of *Liriodendron* have such leaves (*Magnolia*, *Anonaceae*, etc.), but there is a progressive simplification and reduction in lobation as we proceed back in time, the most primitive known forms having ovate or oblong simple leaves (*fig. 3*). We find in the growth of our modern *L. Tulipifera* a parallel development, from the youngest entire or merely notched forms to those of the mature, typically lobed leaves.

Generally speaking, no significance can be attached to the form of the cotyledons; but in this case they represent almost exactly the form we imagine to have been assumed by the primitive *Liriodendron* leaf, which grew in the early Cretaceous or Jura-Cretaceous. (See *Torrey* 2: *pl. 1. figs. 6-8. 1902.*) We picture this ancestor as a tree with simple, ovate or lanceolate leaves, short petioled and without stipules or bud-scales. The vernation of the leaves was probably conduplicate, as in the existing *Magnolia*, it being obviously improbable for it to have been reflexed in the ancestor of short-petioled leaves such as those of *Liriodendron simplex* and *L. primaevum*. We consider that this entire, oblong form of leaf, tapering at both ends to a blunt point, was succeeded by a series of forms ranging from *Liriodendropsis angustifolia* Newb. at the one extreme, through *Liriodendron simplex* Newb., *L. primaevum*

Newb., and *L. Meekii* Heer, to *L. semialatum* Lesq. at the other.

This more or less closely related group includes four types of leaves. The first, a narrow elongated leaf, with an emarginate apex (*Liriodendropsis angustifolia*), occurs in such numbers in the Amboy clays and is so uniform in shape as to warrant its consideration as at least a permanent variety, which developed from the simple lanceolate ancestral form by a reduction of the apex until it became emarginate in the Lower Cretaceous. The second type includes certain leaves which have been referred to *L. simplex*, and which resemble the preceding in outline, but are somewhat broader. They would have been developed easily from *Liriodendropsis angustifolia* by a slight shortening and broadening of the blade of the latter; and like it, this form is found in the Amboy clays. If we compare some of the figures of *L. simplex* with Lesquereux's *Myrsine crassa*,¹⁴ they seem to be identical.

The third type of leaf is connected with the preceding by insensible gradations from the elongated emarginate forms, showing a constantly increasing width of blade, together with a shortening of its length, the emarginate apex becoming less and less so, until it is simply retuse. If these leaves were somewhat shortened and broadened, they would be identical with the usual form of young leaves of *L. Tulipifera*. If *Phyllites orbicularis* Newb. (Flora Amboy clays, 136. pl. 24. figs. 7, 8) be compared with young leaves of *L. Tulipifera*, they seem very similar and possibly identical. The various fossil leaves referred to *Colutea primordialis* Heer are also of this type, and the same may be said of *Sapotacites retusus* Heer.¹⁵ The resemblance of these ancient *Liriodendron* leaves to various leaflets of existing Leguminosae has also been noted by several authors. We have found many specimens of *L. Tulipifera* leaves that belong here, which shows conclusively that these ancient leaves are true *Liriodendron* leaves. This type is represented by various fossil

¹⁴ Flora Dakota group, pl. 52. figs. 2, 3.

¹⁵ See Flora of Amboy clays, pl. 53. figs. 5, 6.

forms referred to *L. simplex* and *L. primaevum* Newb., showing every gradation in form from the elongated notched leaves through the typical *L. simplex* to the broad forms of *L. primaevum*, which show a tendency to develop four lobes, a stage reached in *L. Meekii* Heer. The typical forms of *L. primaevum* are later in point of time than *L. simplex*, being found in the Dakota group, which forms the lowermost layers of the Upper Cretaceous; while *L. simplex* begins in the Amboy clays, long thought to be the same age as the Dakota, but now referred to some of the later Potomac series (Albirupean) of the Lower Cretaceous. However, many of the forms which have been referred to *L. simplex* are intermediate between it and *L. primaevum*, there being no very clear lines of demarkation among *Liriodendropsis angustifolia*, *Liriodendron simplex*, *L. primaevum*, and *L. Meekii*; each being a modification of the preceding through insensible gradations. It is but a step from some forms of *L. primaevum* to *L. Meekii*, and we have among our collections of *L. Tulipifera* many leaves that approximate those of *L. Meekii* in shape.

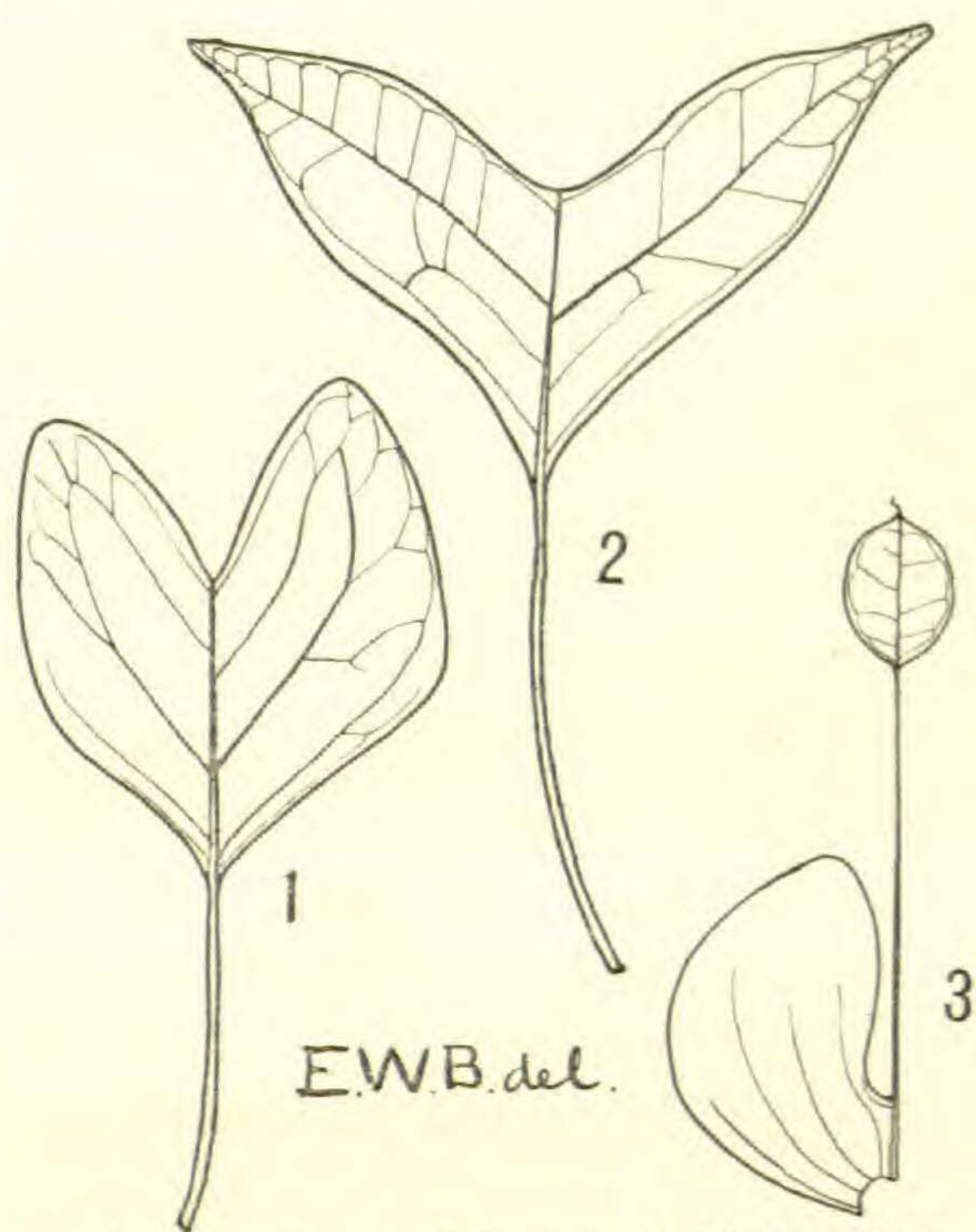
The fourth type of this group represents the other extreme of form, and is somewhat removed from the preceding three. It preserves the pointed apex of the original ancestor, which gradually broadened until it developed an obtuse basal lobe on each side. This form is represented among our known fossil forms by *Liriodendron semialatum* Lesq., and among leaves of *L. Tulipifera* by several specimens. *L. semialatum* is found in the Dakota group, and would have had ample time to develop into a broader leaf with basal lobes during the long period of the Lower Cretaceous when the Amboy clays were being deposited along our eastern coast. The small leaves from the Upper Cretaceous of Vancouver island, described by Dawson as *L. succedens*, if they belong to this genus would be the natural descendants of *L. semialatum*.

If we call the theoretical oblong-lanceolate form *stage 1*, the preceding five closely related leaf types fall naturally in a group which may be called *stage 2*.

Somewhat aside from the preceding are those forms included in *Liriophyllum*, a genus established by Lesquereux in 1876¹⁶ to contain certain leaves from the Dakota formation evidently allied to *Liriodendron*. They are somewhat coriaceous in texture, with obscure venation, and differ widely in outline from any known forms of *Liriodendron*, being (except *L. obcordatum*, which is probably not a *Liriophyllum* at all) square or broadly rhomboidal in general outline, and split at the apex along the line of the midrib about half way to the base, the two lobes being sublobate or bilobate, and separated by an obtuse sinus. Just what is the relation between these leaves and *Liriodendron* is hard to say. We know of no forms of *Liriodendron*, either ancient or modern, that approach very closely the peculiar shapes of *Liriophyllum populoides*, and *L. Beckwithii*. *Fig. 1* shows the nearest form to *Liriophyllum* I have been able to find in some ten years collecting. In no case, however, is the resemblance very close, the nearest being those which would be identical with *Liriophyllum populoides* were the base somewhat wider. Bilobate leaves with a deep, wide sinus at the apex are common enough, the leaves tending to assume that form in the vicinity of flowers, or where the nourishment is defective; but none of them show any tendency to widen at the base, or contract the width of the sinus as in the leaves of *Liriophyllum* (*fig. 2*). There are two forms of *Liriodendron* leaves, either of which I conceive could have been ancestral to *Liriophyllum*. One is the common form of young leaves on modern shoots, and needs but to become parted farther down along the midrib, and to more largely develop the basal and apical lobes, to be a true *Liriophyllum*. The other is some form similar to *Liriodendropsis angustifolia*, which, by a shortening and widening of the blade, through some such form as *Liriodendron alatum*, might lead to *Liriophyllum*. Of the two, the latter seems to be the more tenable, for the orbicular notched leaves, first mentioned above, have never been found in the fossil state, unless *Phyllites orbicularis* may be so considered. It requires but a slight enlargement

¹⁶ Hayden's U. S. Geol. and Geog. Survey, p. 482.

of *Liriodendropsis angustifolia* to secure a form similar to *Liriodendron alatum*, and by a slight shortening and broadening of the blade in the latter we obtain a form from which it is an easy transition to *Liriophyllum populoides*, through forms with slightly more ascending apical lobes, and with a greater development of the basal portion of the blade in a lateral direction. I would consider *Liriophyllum obcordatum* as co-laterally descended from some simple ovate form such as some of the forms referred to *Liriodendron primaevum*. In either case, a lengthening of the next to the last pair of primaries, and the resulting lobes, would give a form identical with *Liriophyllum obcordatum*. However, we do not consider this a true species of *Liriophyllum*; it is either a young and anomalous *Liriodendron* leaf, or a



Certain forms of leaves of *Liriodendron Tulipifera*.

leaflet of some species of Leguminosae, preferably the former.

Liriophyllum populoides, the type of the genus, as the winged margins of the petiole show, had advanced several stages in the development of stipules. It is undoubtedly related to the ovate simple forms of the ancestral leaf through a form similar to *Liriodendron alatum*, as was just pointed out, possessing, as it does, the winged petioles of the latter. Lesquereux's two figures of *Liriophyllum populoides* have the petioles broken off, but both show the petiole widening as it descends. In the figure of a young leaf, the wings are in juxtaposition with the leaf blade, while in the older leaf there is an interval of petiole, apparently showing that the wings grew down the petiole as it lengthened. The immature leaf furnishes additional proof of its origin from

a form without the widely spreading base, showing ascending margins, and with but an indication of the spreading basilar extensions or lobes which characterize the mature leaves.

Liriophyllum Beckwithii is either an abnormal form of *L. populoides*, or a further extension and more pronounced development of its salient characters. Of rare occurrence and large size, it may simply represent a leaf of *L. populoides* of extraordinary size and more extensive lobation, induced by favorable conditions of growth, just as we find extraordinarily developed leaves of large size and extensive lobation on especially vigorous shoots from saplings of *L. Tulipifera*.

Sterile soil, lack of humidity, or some similar hard condition may account for the development of the *Liriophyllum* type of leaf. The following facts would seem to imply this: In *L. Tulipifera*, the leaves on the same twigs as the flowers tend to an abbreviated blade. Again, by cutting off the shoots of the year, and forcing next year's buds to take their places, we obtain leaves similar to the above. All of these forms approximate *Liriophyllum*, and hint at its probable mode of origin. That the peculiar ascending primaries offer no objection to this theory is well shown in several small specimens of *L. Tulipifera* leaves in my collection, with a cleft apex and opposite ascending veins. It would require only the slowly increasing development of an opposite-veined and cleft-tip form like this to become the opposite-veined, deeply cleft *Liriophyllum*.

As the Dakota time progressed, *Liriodendron*, fostered by the humid and warm Cretaceous climate, developed rapidly, the leaves increasing greatly in size, and with this went increased lobation, the tendency being for those portions of the leaf blade at the terminals of the secondary veins to increase at the expense of the rest of the blade. These lobes are obtuse where a full or an extra supply of nourishment is obtained, and acute where there is any diminution of the supply. That the congenial warmth, humidity, and rich soil of this period were the primary factors in the great variation and development of the *Liriodendrons* is undoubtedly the case; for in modern tulip trees those

growing in rich soil, or leaves on especially vigorous shoots from old stumps, saplings, etc., show the greatest tendency to variation and large size, and trees in poor soil have smaller acutely lobed leaves, and the leaves on large, mature trees are smaller than those on saplings, and have the lobation reduced almost to cuspidate points. Again, on individual shoots where the supply of nourishment is reduced artificially, or where it is diverted for the formation of flower and fruit, the leaves undergo great reduction in size and lobation, showing a tendency to assume a two-lobed, *Liriophyllum*-like form. There is nothing particularly new in this view, for we find in Lindley's *Introduction to Botany* (p. 136, 1839) the following: "Lobation [of leaves] is deepest and more pronounced in those individuals of the same species whose vegetation has been least favored by humidity, and the nature of the soil."

Large leaves, affording a larger assimilating area, are of course more advantageous in the performance of the functions of vegetation than smaller ones, and some of the additional advantages accruing when these large leaves are lobed instead of simple may be enumerated as follows: The simple leaves are more unwieldy and heavier, and therefore much more easily affected and broken by winds and rain. In the lobed forms the sunlight is more completely utilized; there is economy of circulation through more direct connection of parts; there are more leaves to a given amount of material, and therefore more active assimilating organs. The functional activity of two-lobed leaves, having an area equal to that of a single simple leaf, ought to be considerably greater.

The next stage in the genealogy of *Liriodendron* which has been preserved is *L. giganteum* Lesq., which is reached by a series of slight changes from the more primitive *L. Meekii* through constantly enlarging and more lobate forms induced by the environment indicated above. The petiole has become greatly lengthened, and stipules had probably been developed; for, although we have no trace of stipules except in the winged petioles of *Liriophyllum populoides* of the Dakota and *Liriodendron*

alatum of the Laramie, unless certain forms referred to *Paliurus*¹⁷ are the remains of stipules, they must have been developed early in the history of the group, before the vernation became fixed and the petioles lengthened. *L. giganteum* had a very large leaf, 5 by 16.5^{cm}, with consequently large veins, oblique or rectangular, oblong, obtuse lobes, and deeply emarginate apex. We have a number of leaf forms of *L. Tulipifera* from particularly luxuriant saplings that greatly resemble *L. giganteum*. The venation is similar; the general contour is similar, the lobes in *L. Tulipifera* being a trifle less obtuse; and, like *L. giganteum*, these are very large leaves, in fact in all extra large leaves of *L. Tulipifera* the tendency is to assume a form that approximates *L. giganteum* in a general way, and we have a number of such forms in our collection. *L. giganteum cruciforme* Lesq. differs but slightly from *L. giganteum*, the lobes being more nearly at right angles and the intervening sinuses deeper and narrower; the lobes are also somewhat less obtuse and more like some of our specimens of *L. Tulipifera*. Dawson's *L. praetulipiferum* from the Upper Cretaceous is evidently related to *L. giganteum*. It also resembles some of the forms of *L. Meekii*, and is without doubt closely related to the then existing ancestor of our modern tulip tree.

The next species in the geological record is *L. oblongifolium* Newb. from the Amboy clays of New Jersey. Among the various published figures of this species all are fragmentary and of more or less uncertain affinity except one figure which shows a leaf surprisingly like the normal mature leaves of *L. Tulipifera*. In fact there can be but little doubt that *L. oblongifolium* is in the direct line of descent leading to *L. Tulipifera*, from which the latter has changed but slightly. *L. oblongifolium* is somewhat less lobate than the modern leaf, and has the lateral veins nearly straight, ascending, and approximately parallel. There is no doubt that *L. oblongifolium*, *L. praetulipiferum*, and *L. giganteum*

¹⁷ See Flora of Amboy clays, *pl.* 23. *figs.* 8, 9; Flora of the Dakota group, *pl.* 35. *figs.* 6, 7; Bull. Torr. Bot. Club 21: *pl.* 177. *fig.* 5; Trans. N. Y. Acad. Sci. 12: *pl.* 2. *figs.* 12, 18, 19.

were very closely related, and probably had a common ancestor. Among the leaves of *L. Tulipifera* we can find a perfect series from *L. oblongifolium* to *L. giganteum* and *L. praetulipiferum* on the one hand, to *L. quercifolium* on the other. The latter was derived from *L. oblongifolium* through leaves with increased lobation.

The next fossil species is *L. pinnatifidum* Lesq., and we note that Lesquereux's two figures of this species differ considerably from each other in shape. Both are fragments, and their nervation is dissimilar and remote from that which obtains in all the other known forms of *Liriodendron*. While one may be a *Liriodendron*, we are forced to consider the other as an altogether different species, possibly allied to *Quercus*, at any rate not related to *Liriodendron*. We note in passing that Lesquereux's *Cissites obtusilobus*, also from the Dakota group (Fl. Dak. 161. pl. 33. fig. 5), somewhat resembles the species under discussion. Lesquereux¹⁸ wrote later of *Cissites* as follows: "Velenovsky, in his Flora Bohm. Kreideformation, pt. 2, pl. 6. fig. 2, has a figure like this, and has named it *Liriodendron Celakovskii*. It essentially differs in the lateral primaries being basilar." We are inclined to think that this observation is a hint at the true affinity of the specimen, for it has the indefinable look of a *Liriodendron* leaf, and we have in our collection of *L. Tulipifera* leaves several that approximate *Cissites obtusilobus*. *Cissites alatus* Lesq. (Fl. Dak. group, 160. pl. 23. fig. 6. 1891) in all probability also belongs here. Lesquereux was inclined to refer it to *Liriodendron*, and afterward compared it with *L. Gardneri* Saporta, which it greatly resembles. We have also *L. Tulipifera* leaves that resemble it, but somewhat remotely.

The American Cretaceous species of *Liriodendron* at this time diverge somewhat widely from the line of descent leading to the modern form, and develop into some curious lobate forms that will be considered later.

We are obliged to go to Europe to find the stages subsequent to *L. oblongifolium* leading to *L. Tulipifera*. We find them nearly

¹⁸ Flora Dakota group, p. 161, footnote.

complete in the forms variously referred to *L. Procaccinii* Unger, *L. Haueri* Ettings., *L. helveticum* Fish-Oester, *L. islandicum* Sap. & Marion, all from the European Tertiary¹⁹ formations, the forms from the Pliocene being clearly identical with the existing species. Schmalhausen²² refers a leaf from the Pliocene (?) of the Altai mountains to *L. Tulipifera*, and Saporta and Marion consider certain of the forms referred to *L. islandicum* as identical with the modern tree.

With the advent of the Glacial period the European *Liriodendrons*, along with *Sassafras*, *Magnolia*, *Celastrus*, etc., disappeared from that continent, the glacial conditions undoubtedly forcing them southward until further retreat was cut off by the Mediterranean.

Returning to the curious lobate forms from the American Cretaceous, we have four species and one variety that are unlike anything seen in the modern species, and evidently not forming a part of its ancestral line, but a collateral branch from it. The most lobate forms found on the modern tree are quite different from the long, narrow-lobed forms under consideration. The least divergent form is *L. intermedium* Lesq., and it is only known from fragments of the upper part of the leaf. It was evidently a large leaf, and might be derived from a form like *L. giganteum* by an extreme narrowing of the lobes. The next species, *L. Wellingtonii* Lesq., differs from the preceding in having the supposed basal lobes of *L. intermedium* lengthened and curved inward, ascending almost vertically nearly to the tips of the upper lobes. *L. acuminatum* Lesq. differs from *L. Wellingtonii* in having the basal lobes somewhat reduced in length and all of the lobes acuminate. The variety *bilobatum* merely differs from *L. acuminatum* in having the basal lobes bilobate, thus greatly resembling various forms referred to *Aralia*. Lesquereux compares it with *L. islandicum* S. & M. If it be a true *Liriodendron*

¹⁹ Diligent search fails to disclose *Liriodendron* in the extensive European Cretaceous system.

²⁰ Ueber tertiäre Pflanzen aus dem Thale des Flusses Buchtornia am fusse des Altaigebirges. *Palaeontographica* 33. 1887. *L. Celakovskii* Velen. is probably not a *Liriodendron* (Bull. Torr. Bot. Club, July 1902).

it is certainly a very anomalous form of leaf, and represents the extreme of development of the lobate leaf in this genus.

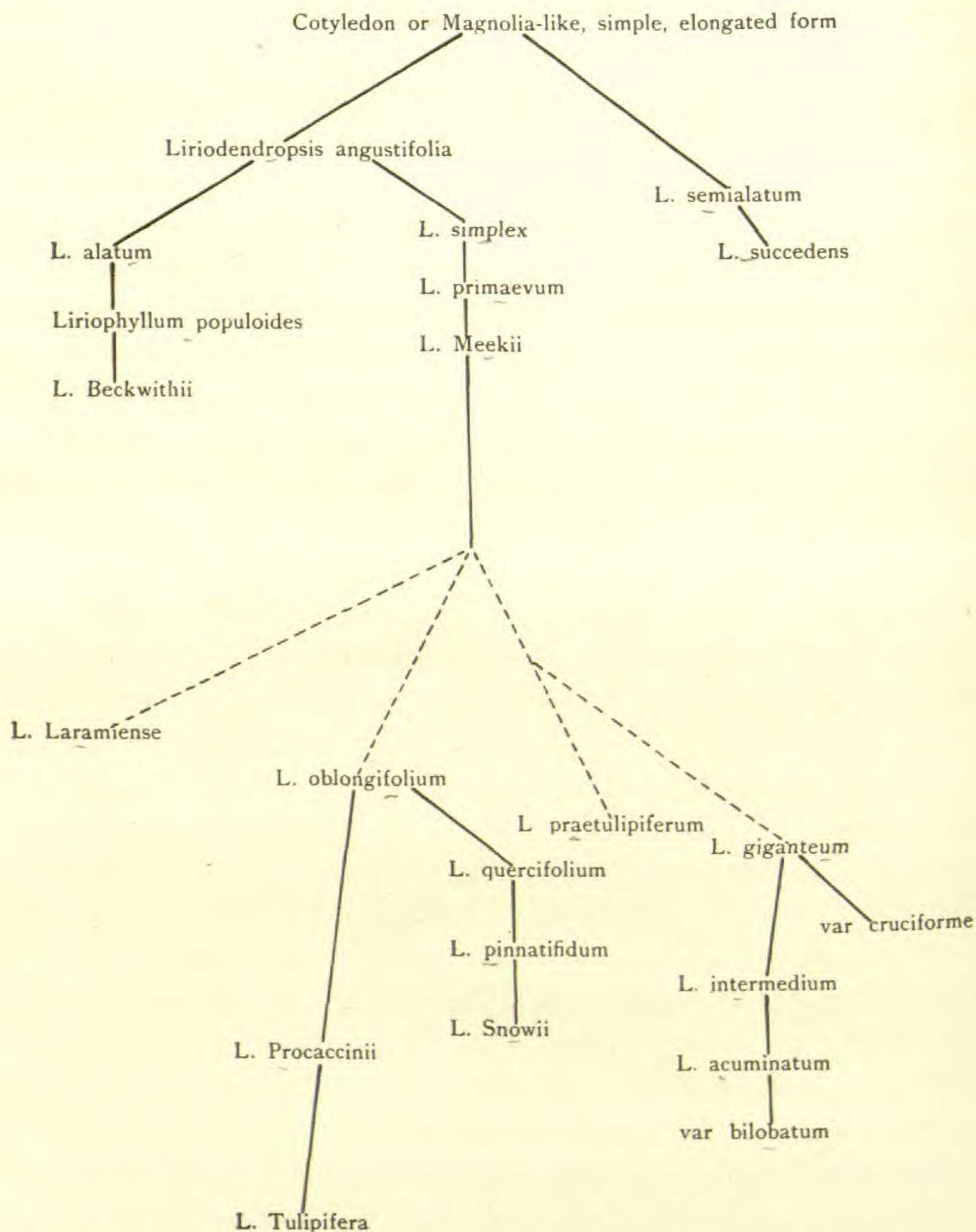
We have next to consider Ward's *L. Laramiense*. It is a more recent species than any of the preceding American forms, being from the Laramie. According to Stanton & Knowlton,²¹ these strata underlie marine Cretaceous and therefore belong to the Montana formation. If this reference be correct, it leaves but one American species besides the existing one subsequent to the Cretaceous. If *L. Laramiense* is a true species, the doubt being caused by the known remains consisting of but the basal fragment of a leaf, it was a comparatively simple form which developed from the ancestral *Tulipifera*-like form, which was probably contemporaneous with it, although as yet no *L. Tulipifera* remains have been found in these strata. Modern simple *L. Tulipifera* leaves similar to *L. Laramiense* are very common.

The last fossil form to consider is the remarkable *L. Snowii* Lesq., from the Dakota group. It is a large leaf, ovate in outline, pinnately divided into several linear, obtuse lobes on each side, which are attached by their whole bases to the midrib, but are entirely separated from each other by a considerable interval of free midrib. While it differs so widely from any of the other forms of *Liriodendron* as to seem to represent an unallied compound leaf, there is something about it that stamps it as a species of *Liriodendron*. The venation is also typical of the genus. It may represent a further and extreme development from *L. pinnatifidum*, which originated, flourished, and disappeared during the deposition of the Dakota group; we certainly have nothing like it among modern *Liriodendron* leaves.

With the close of the Dakota period the *Liriodendron* group seems to wane, having but one or possibly two species in the Laramie, and none in the American Tertiary or more recent formations, although the tulip tree flourished in Europe throughout the Tertiary. While the extremely lobate species may have

²¹ Bull. Geol. Soc. Am. 8: 127-156. 1896.

become extinct after the close of the Cretaceous, it is very probable that the ancestors of the modern tree still flourished, and we can only blame the imperfect geological record for the lack



of evidence of their existence. It would seem that the numerous Tertiary lakes would have furnished abundant facilities for fossilizing leaves from the trees that skirted their shores, or were brought down from the adjacent uplands by the many streams.

Matthew and Davis²² have recently advanced reasons for considering a considerable number of the so-called Tertiary lake formations to be flood-plain and aeolian deposits. If their arguments are sustained, which seems unlikely except for restricted areas, the absence of leaves from these formations becomes explicable. Be this as it may, the record has thus far proved barren, and we can only congratulate ourselves that the more ancient record is so complete. We can better spare the record of the Tertiary, for the modern form became practically fixed in *L. oblongifolium* of the Amboy clays, or its undiscovered, closely related contemporary, and has changed but slightly in subsequent times.

A summary of these suggested relationships may be presented as on opposite page.

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²² MATTHEW, W. D. Bull. Am. Mus. Nat. Hist. 12: 25. 1899; GILBERT, G. K. 17th Ann. Rep. U. S. Geol. Surv. 1895-6, part 2, p. 575; WILLISTON, Kan. Univ. Geol. Surv. Rep. 1896; see also FRAAS in Science 14: 210.